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THE RELATIONSHIP OF ISLAND AREA AND
ISOLATION TO COLOR
POLYMORPHISM IN *LIGUUS FASCIATUS*
(PULMONATA, BULIMULIDAE)

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ABSTRACT. *Liguus fasciatus* is a highly polymorphic arboreal pulmonate living on small islands called hammocks in the Florida Everglades. Color variation in this snail has in other studies been assumed to be random and of no selective significance. Multiple regression analysis showed that hammock area was a statistically significant predictor of color morph diversity, and that measures of isolation were either insignificant or significant but subordinate to the effect of area. From this result it was inferred that color variation in *Liguus* was regulated by available ecological diversity (hammock area) even when interhammock migration appeared to be extensive. Color polymorphism in this snail might be imposed by visual predation, larger hammocks with more heterogeneous floral composition having more morphs because they offer more possibilities for cryptic or aposematic associations to avoid predators.

INTRODUCTION

Conchologists have long considered color variation in the remarkably polymorphic *Liguus fasciatus* to be random and of no adaptive significance. "On the whole it is not apparent that any form of selection has been a major factor in the evolution of Florida *Liguus*" (Pilsbry 1946: 47). Ecological uniformity of habitats led Pilsbry (1912, 1946) to attribute differences in color and form between monomorphic colonies to isolation alone, and to explain variation in mixed colonies by random mutation and recombination of hypothetical Mendelian alternatives.

However, recent studies indicate that random genetic events do not, as once thought, constitute the most important mode of evolution in land snails. Crampton's (1916, 1925, 1932) contention that intraspecific variation in *Partula* was due to genetic

drift has been contested by selectionists both on the basis of his collecting methodology (Mayr 1942; Cain and Sheppard 1950; Ford 1964) and on reexamination of his own data (Bailey 1956). Gulick (1873, 1905) was unable to correlate variation in *Achatinella* with ecological diversity, but Welch (1938, 1942, 1958) found changes in both color and form with altitude in achatinellids when temperature and moisture gradients were pronounced. Diver (1940) and Lamotte (1952) proposed that color variation in *Cepaea nemoralis* resulted from genetic drift, though it is now evident that relative frequencies of color and banding patterns in *Cepaea* are regulated to some extent by visual predation (review in Cain and Sheppard, 1954) and climatic factors (Lamotte 1959, 1966; Wolda 1967; Arnold 1968, 1969). Furthermore, Murray (1964) demonstrated that hermaphroditism, sperm storage, and multiple matings in *C. nemoralis* function to maximize effective population size, thereby reducing the probability of genetic drift in small colonies. Gould (1969) disclosed the adaptive significance of both color and form in his study of temporal character variation in *Poecilozonites*.

In the present paper I show that the number of color morphs in populations of *Liguus fasciatus* living on small islands can be predicted by island size and isolation. It is suggested that polymorphism in this snail is maintained by a selective balance of phenotypes.

Liguus is particularly suitable for investigating effects of environmental factors on phenotypic diversity. The snail lives on small islands called hammocks in the Florida Everglades. Hammocks are slightly elevated remnants of Pleistocene coral reefs that support a tropical hardwood vegetation. They are surrounded by sparse pine woods or swamp, both of which are inhospitable to *Liguus*. Thus, habitat size and distance between individual populations are well defined and easily measured.

LIGUUS MATERIAL

Liguus colonies, once abundant in Florida, have now been decimated to near extinction by land clearing, glade fires, amateur collectors, and introduced rats. Fortunately, a few careful investigations were carried out before the onslaught. Material used in this study came from extensive collections made by W. J. Clench and W. S. Schevill during February and March, 1931, from an assemblage of hammocks on Long Pine Key, Dade County, Florida (Fig. 1). The hammocks ranged in size

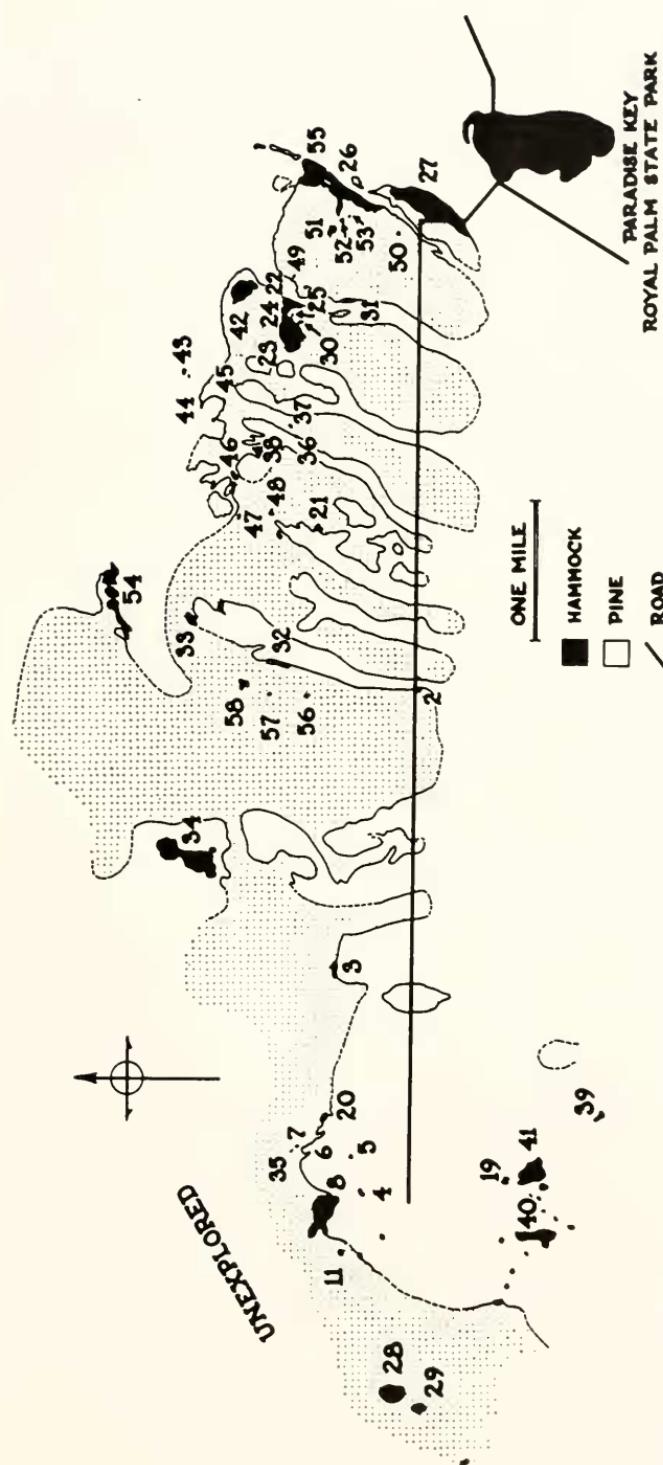


Figure 1. Distribution of hammocks in Long Pine Key, Florida. Area left blank is glade. *Lignus* material was available only for those hammocks which are numbered.

from 0.34 to 43.80 acres. According to Clench (personal communication), an endeavor was made to collect samples of all the varieties present in each hammock visited, but not necessarily in proportion to their natural frequency distribution (non-random). The material, comprising several thousand shells from 48 hammocks, was sorted by Clench as to varieties and placed in the mollusk collections of the Museum of Comparative Zoology, Harvard University.

I have considered the Long Pine Key material to include nine color morphs, which are described briefly below. The morphs clearly have some genetic integrity. By examining several clutches of eggs, Pilsbry (1946) showed that separate patterns segregated out, but the exact extent to which this occurs is unknown. Pilsbry (1946) classified the morphs of *L. fasciatus* into subspecies, forms, and varieties. The subspecific designations represented different color patterns and had no geographic connotation. The forms were based on the colors present in the patterns and the presence or absence of pink coloration on the early whorls and columellar callus. The varieties were usually named stages in the continuous variation present in the forms. His system for sorting out morphs is convenient and I have largely adhered to it here. But the genetic criteria on which his hierarchy was based are unacceptable. For instance, the rare variety *deckerti* (see below) found in three widely separate localities in Florida was thought to have arisen from the form *castaneozonatus* through mutational "loss" of the factor for pink coloration (1946: 70). Its white apex and columellar callus could, however, be the result of a number of conceivable schemes involving matings with morphs having white apices, dominance interactions, recombination, and close linkage. The genetic mechanisms governing coloration in these snails are probably complex and I have chosen not to make any underlying assumptions about them. For purposes of this paper it is sufficient to recognize that *L. fasciatus* is a highly variable species in which more or less disjunct color morphs can be discerned and that the number of morphs present in a population is some indication of its genetic variance.

MORPHS PRESENT IN LONG PINE KEY

Names listed are those used by Pilsbry (1946) and the patterns refer to Figure 2.

1. *eburneus*: shell completely white.

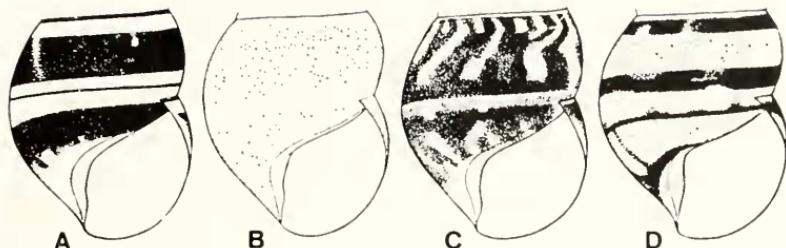


Figure 2. Basic color patterns for *Liguus fasciatus* present on Long Pine Key, Florida (from Pilsbry, 1946). See text for explanation.

2. *cingulatus*: faint yellow spiral zones (Pattern A) on a white background; apex and columellar callus white.
3. *roseatus*: yellow spiral zones (Pattern A) on a white background; apex and columellar callus pink.
4. *castaneozonatus*: splotchy to solid brown spiral zones (Pattern A) on a white background; apex and columellar callus pink.
5. *deckerti*: brown spiral zones (Pattern A); apex and columellar callus white.
6. *luteus*: uniform faint yellow coloration (Pattern B); apex and columellar callus white.
7. *ornatus*: uniform yellow coloration (Pattern B) intensifying to amber near the lip; apex and columellar callus pink.
8. *testudineus*: variegated and banded (Pattern C or D), with brown coloration on white to yellowish background; apex pink with pink or white columellar callus.
9. *marmoratus*: variegated and banded (Pattern C or D) with brown coloration on a white background; apex and columellar callus white.

Patterns C and D are endpoints of continuous variation, the dense variegation or "flames" of C gradually superimposing the bands and lightly variegated pattern in D. There appear to be no good objective criteria for discriminating various stages in this continuous variation. Thus, the distinction between morphs 9 and 10 is one of apical coloration.

METHODS

Computerized stepwise multiple regression analysis using program BMDO2R (Dixon, 1968) was performed to determine whether the degree of polymorphism in populations from dif-

ferent hammocks correlated with any of several independent variables measuring area or isolation.

No general discussion of the estimating equations of multiple regression is presented here as they have now been so extensively employed in ecological studies (cf. Ebeling *et al.*, 1970; Hamilton *et al.*, 1963; Hamilton *et al.*, 1964; Hamilton and Rubinoff 1963, 1964, 1967; Johnson *et al.*, 1968; Pomeroy, 1967; Vuilleumier, 1970).

The methodology allows one to determine both whether a statistically significant prediction of the dependent variable can be made using some or all of the independent variables, and which independent variables are most important. The square of the multiple correlation coefficient R^2 estimates the amount of variance in the dependent variable explained by the combined effects of the independent variables. The significance of the entire regression was tested by the variance ratio F , which is the mean square due to regression divided by residual mean square. The significance of the contribution of each independent variable to the total explained variance in the dependent variable (R^2) was tested by using the t -ratio, which equals the partial regression coefficient divided by the standard error (Snedecor and Cochran, 1967). Three versions of the regression were carried out: a linear model, a semi-log model using log-transformed independent variables, and a log-log model.

The dependent variable was simply the number of morphs present on each hammock. Independent variables were restricted to those which could be measured from a large map of the collecting site prepared by W. S. Schevill (Fig. 1). Previous studies in island biogeography, in which multiple regression models were used to predict species diversity (cf. esp. Hamilton and Rubinoff 1963, 1964, 1967; Vuilleumier 1970), suggested several independent variables. The following were tested for their ability to predict the number of morphs: (1) Hammock Area. This variable is commonly used as an index of ecological diversity. Larger hammocks were expected to have more micro-habitats; i.e., more plant species, more possibilities for cryptic associations, greater foliage height diversity, etc. (2) Distance to Hammock 27. Hammock 27 (Fig. 1) was the largest island and may have been an effective dispersal center for the entire group of hammocks even though it was peripherally located. It also had the fortuitous advantage of being close to Paradise Key, an enormous hammock which probably exerted influence over

the morph diversity of Long Pine Key hammocks, but which was not included in this study because data on the number of color morphs present were unavailable. This variable tested effectiveness of isolation from a possible source area of high phenotypic variability. Hammock 27 had eight of the nine color morphs. Three additional variables determined the effects of isolation in a more localized sense. (3) Distance to the nearest large hammock, a large hammock being defined as any of hammocks 54, 23, 26, 8, 34, 27. (4) Distance to the nearest hammock. (5) Size of the nearest hammock.

RESULTS

The relative influence of each independent variable and an analysis of variance are given in Table 1. In all three models hammock area was the most significant ($P < .001$) predictor of the number of morphs present. Area made a higher contribution to R^2 in the semi-log model (.39) than in the linear model (.30), an indication that the data are somewhat curvilinear with respect to area.

Variables measuring isolation, with the exception of distance to hammock 27, proved to be insignificant. Distance to hammock 27 made a significant contribution to R^2 in the linear ($P < .05$) and semi-log ($P < .025$) models. This suggested that a slight phenotypic diversity gradient extended westward from hammock 27. If hammock 27 was, or was near, the effective population center, then perhaps the population was simply expanding westward. There was some evidence to support this contention in the distribution of individual morphs. Two morphs, *ornatus* and *marmoratus*, did not extend farther west than hammocks 34 and 56 respectively and *deckerti* was confined to hammocks 55 and 26. They were the least frequent in occurrence and were found predominantly on large hammocks. These morphs might still have been in the process of dispersing westward. When they were removed from the analysis, the number of morphs still correlated significantly with hammock size ($.01 \geq P \geq .001$). But distance measures correlated so poorly when added to the multiple regression models that the significance of the entire regression was reduced to $P < .05$ in the linear and log-log versions. Otherwise, the morphs showed no evident propensity for east or west. Even though distance to hammock 27 made a significant contribution to R^2 , its effect was clearly subordinate to that of area.

TABLE 1. Relative influence of independent variables and analysis of variance for multiple regression equations used to predict the number of color morphs in populations of *Ligia fasciatus* living on hammocks.

Independent variables	<i>Linear Model</i>			<i>Semi-log Model</i>			<i>Log-log Model</i>		
	Contribution to R^2	t(42)	P*	Contribution to R^2	t(42)	P	Contribution to R^2	t(42)	P
X_1 Hammock area	.3013	4.5705	< .001	.3876	4.6934	< .001	.2895	3.6073	< .001
X_2 Distance to hammock 27	.0662	2.2924	< .05	.0925	2.5184	< .025	.0297	1.3450	> .10
X_3 Distance to nearest large hammock	.0166	1.1729	> .20	.0017	.3782	> .50	.0011	.2569	> .50
X_4 Distance to nearest hammock	.0050	.5218	> .50	.0036	.6214	> .50	.0011	.3205	> .50
X_5 Size of nearest hammock	.0010	.2604	> .50	.0031	.5053	> .50	.0034	.4415	> .50
Total R^2	.3901			.4885			.3248		
Analysis of variance for entire equation	$F_{(5,42)}$	= 5.372, P < .01		$F_{(5,42)}$	= 8.022, P < .01		$F_{(5,42)}$	= 4.041, P < .01	

*P = Probability that calculated values result from chance. All other symbols discussed in text. Subscripts represent degrees of freedom.

Regression equations are:

$$\begin{aligned} \text{Linear model, } Y &= 3.8164 + 4.3240X_1 - 0.0463X_2 + 0.1264X_3 - 0.1277X_4 + 0.2654X_5; \\ \text{Semi-log model, } Y &= 7.2483 + 1.8446 \log X_1 - 1.0776 \log X_2 + 0.1250 \log X_3 - 0.3262 \log X_4 - 0.1850 \log X_5; \\ \text{Log-log model, } \log Y &= 0.8701 + 0.2125 \log X_1 - 0.0863 \log X_2 + 0.0127 \log X_3 - 0.0252 \log X_4 - 0.0242 \log X_5; \end{aligned}$$

It is worth noting that in three cases independent variables measuring isolation had significant simple correlation coefficients with the number of morphs: 1) distance to the nearest large hammock, $r = -.407$, $P < .01$; 2) distance to hammock 27, $r = -.398$, $P < .01$, both in the semi-log model; and 3) distance to the nearest large hammock, $r = -.310$, $P < .05$ in the log-log model. These isolation variables were de-emphasized in the multiple regression analyses because they did not correlate with the dependent variable as significantly as area ($r = .549$, $.538$, $.623$, $P < .001$, in the linear, log-log, and semilog versions respectively), did not explain as much of the variance in the dependent variable as area, and were partially redundant with one another.

Associations between intraspecific variability, interspecific competition, faunal diversity, etc. and various physical or biological environmental parameters are often obscure. The usefulness of multiple regression lies in the ability to discern a hierarchy of importance among independent variables relating to some dependent variable from a matrix of correlations between all variables. In this particular study it indicated that hammock area was more important than isolation in predicting the amount of color variation in populations of *L. fasciatus*. It is possible, however, that the distance measurements and transformations used may not have been the relevant ones for predictive purposes.

MacArthur and Wilson (1967: 132-133) concluded on the basis of theoretical considerations that in colonization "stepping stones" should be less important to passive dispersers than to active dispersers. Snails probably disperse passively and one would expect direct distance measurements to be most appropriate in this kind of study. When hammock-hopping distances¹ were tried in place of variables 2 and 3, however, the results remained very nearly the same as those presented in Table 1. R^2 for the linear, semi-log, and log-log model was .39, .51 and .34 respectively, and probability levels for significant variables were identical, with the exception of variable 2 in the semi-log model which was significant at $P < .005$ instead of $P < .025$.

¹Hammock-hopping was measured by using intervening hammocks as stepping stones rather than using direct distance. Also, measurements were made through the pine wood or to the narrowest passage through glade if glade must be crossed, the assumption being that it would be difficult for an actively dispersing pulmonate to cross bodies of water.

(a difference of less than .02 in the contribution of variable 2 to R^2).

Distinction in mode of dispersal that might otherwise be indicated by using either direct or hammock-hopping distances could be blurred by the small size of the study area as a whole. Predatory birds and high winds are likely agents of dispersal and they probably transport snails a highly variable range of distances. Simpson (1929) occasionally found live *Liguus* far into the open pine wood which he thought were propagules on their way to colonize new hammocks. He gives a delightfully anthropocentric account of *Liguus* "obeying an instinct for founding new colonies." It seems more likely that the snails he found were dropped by birds.

An analysis of variance for the entire regression for each model is given in Table 1. All three models provided significant ($P < .01$) results. The best predictive value (highest R^2) was afforded by the semi-log model. In all models, however, at least half of the variance in the number of morphs was left unaccounted for. This "error" ($E = 1 - R^2$) was due to several factors. First, there were undoubtedly important variables that were not considered simply because the data were unavailable. For instance, more precise measurements of ecological diversity such as the number and kind of plant species occurring on each hammock may have been important. Secondly, there were errors in measuring the independent variables used in the appraisal of polymorphism. Some morphs must have been occasionally overlooked during collecting. Finally, there is the certainty that not all of the variance could ever be attributed to ecological parameters, part of it being due to genetic mechanisms such as balanced polymorphism (heterozygote superiority) and part of it actually being random.

DISCUSSION

I infer from the inability of isolation to predict the number of color morphs and the widespread distribution of the morphs in general that interhammock migration, however it occurs, is a fairly frequent event, but that its contribution to maintaining polymorphism in *Liguus* is strongly mediated by hammock area. The question now arises: Why is hammock area a good predictor of color variation? A speculative hypothesis is the following.

Boettger (1931) first suggested, without giving supporting data, that the degree of color polymorphism in *Cepaea* is regulated by background heterogeneity through selection by visual predation. The quantitative studies of Cain and Sheppard (see review 1954) corroborated Boettger completely. More diverse backgrounds such as hedgerows, rough herbage, and mixed deciduous woods supported more variable populations of *Cepaea* than the more uniform beechwoods or short turf. Further, cryptic associations between color morphs and background color appeared to confer a selective advantage in eluding predators. For instance, in a study of *Cepaea* in Wytham Woods, Sheppard (1951) found that brown and pink morphs were at an advantage in mid-April when the forest floor was brown, the more conspicuous yellow morphs being selectively predated by thrushes. In May when the forest became green the reverse situation obtained, yellow then being at an advantage.

A similar mechanism might regulate morph diversity in *Liguus*. Larger hammocks with greater foliage height diversity and a greater number of plant species might provide more possibilities for cryptic associations to avoid predators. Natural predators of *Liguus* include the opossum (Pilsbry, 1946), the crow, and "other large birds" (Simpson, 1929). Colonies on small hammocks having limited floral heterogeneity might continually have morph diversity depleted by predators.

Eisner and Wilson (1970) recently suggested the obverse of this hypothesis: that coloration in *Liguus* is aposematic (rather than cryptic). When disturbed the snail withdraws into its shell and discharges large quantities of liquid. Simpson (1929) thought this fluid secretion enabled the snail to slip from the beaks of predatory birds, but Eisner and Wilson believed it to be a chemical defense mechanism. The success of cryptic or aposematic coloration depends on suitable background color. Since none of the wide variety of morphs will appear conspicuous in all situations, perhaps the snail employs a mixed strategy involving both kinds of coloration. Further observations are needed.

The possibility of low morph diversity on small hammocks being due to genetic drift is not discounted, but seems unlikely for reasons presented against Pilsbry's argument below. Other hypotheses, such as regarding polymorphism as a manifestation of niche subdivision (Van Valen 1965), are conceivable, but lack substantiating evidence.

An explanation for the previously noted curvilinearity of the data with respect to area might be that the number of cryptic associations utilized by this snail is attained at intermediate hammock size, and the probability of adding a new and different association with further increase in area is negligible.

Pilsbry's argument that variation in *Liguus* is random seems untenable for the following reason: Interhammock migration, as already mentioned, appears to be quite extensive. Since the snail is hermaphroditic and has multiple matings a single fertilized immigrant can introduce considerable variation into a colony (Pilsbry, 1912, found at least three separate morphs in one clutch of nine eggs from a single adult). In the early stages of colonization, larger hammocks might be expected to have populations with greater morph diversity simply because they represent larger target areas for propagules; this might be the case with *ornatus*, *marmoratus*, and *deckerti*. The great abundance of *Liguus* at Long Pine Key and further north in Florida suggests, however, that the snail has populated southern Florida for a rather long period of time, possibly since the last glaciation, and that it has essentially achieved a steady state. This being the case, and if variation occurred randomly and were unaffected by selection, then there would be no reason to expect populations living on larger hammocks to be more variable than those living on smaller ones. The highly significant positive correlation of hammock area and the number of morphs ($P < .001$) indicates, however, that morph diversity on smaller hammocks is maintained at a low level. Visual predation might be an important selective agent reducing variation on small hammocks. Visual predators are known for *Liguus* and a similar mechanism has been shown to operate with another polymorphic pulmonate.

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